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RECEPTIVE FIELDS OF OPTIC NERVE FIBRES IN THE SPIDER MONKEY

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Our present knowledge of how mammalian retinal ganglion-cell receptive fields are organized is based mainly on findings in the cat by Kuffler (1953). These results have since been confirmed and extended (Barlow, FitzHugh & Kuffler, 1957; Hubel, 1960; Wiesel, 1960), but up to now similar studies have not been made in primates. The retina of the monkey is of interest, since in most species, including *Ateles* (spider monkey) and *Macaca mulatta*, it is deeply pigmented and has a well defined fovea. It appears to be much closer to the human retina than to that of the cat, which has a highly reflectile tapetum and lacks a fovea. The purpose of this report is to describe the receptive fields of single optic nerve fibres in the spider monkey. In view of the monkey's ability to discriminate colours, some observations were also made on ganglion cell responses to monochromatic stimuli.

METHODS

The four young spider monkeys (8–10 lb., 3·6–4·5 kg) in this study were prepared in a manner similar to that described for the cat (Hubel & Wiesel, 1959). An animal was anaesthetized with thiopental sodium and light anaesthesia was maintained throughout the experiment. The head was placed in a Horsley–Clarke stereotaxic instrument designed to permit stimulation of almost any part of the visual field (Talbot & Marshall, 1941). The eyes were immobilized with the muscle relaxant succinylcholine: this made it necessary to use artificial respiration. The eyelids were held open and contact lenses protected the corneas. The pupils were dilated and accommodation was relaxed with atropine. A slit retinoscope was used to determine the correct supplementary lenses for focusing the eyes on a screen at a given distance.

The animal faced a large tangent screen. This was generally placed 1·5 m from the monkey, but for the smallest stimuli it was moved to a distance of 10 m. A distant tungsten lamp supplied a diffuse background light which produced on the screen a variable luminance of up to 2·0 $\log_{10}$ cd/m^2. Circular or annular spots provided by a tungsten projection lamp could be shone on different parts of the screen. The maximum spot luminance was 3·0 $\log_{10}$ cd/m^2. Stimulus spots were adjusted in intensity with an iris diaphragm so as not to exceed the background by more than 2 $\log_{10}$ units. At 10 m distance spots were obtainable subtending angles down to about 20 sec of arc, equivalent to about 2 μ on the retina. Fifteen interference filters (Farrand Optical Co., New York, N.Y.) ranging from 400 to 700 mμ with a band width at half maximum transmission of 25–50 mμ, were used to obtain coloured

stimuli. The coloured lights were not calibrated for equal energy, but this was not necessary for the observations to be described.

By a projection method points corresponding to the optic disk and the fovea were mapped out on the screen. An ophthalmoscope was designed which permitted direct vision of the fundus by means of a small spot of light. This spot was directed through the centre of the pupil at the fovea or optic disk and the instrument was locked in position. The ophthalmoscope shone a second beam in a direction exactly opposite to the retinal beam, making a small spot on the screen. The position of this spot then corresponded to the illuminated retinal point. Points on the screen could thus be specified with reference to the fovea and the optic disk, and points on the retina were stimulated by illuminating the corresponding points on the screen. The correspondence could be verified by illuminating a point on the screen (e.g. that corresponding to the optic disk) and observing the retina directly with an ordinary ophthalmoscope through a half-silvered mirror placed at 45° in front of the eye.

Regions in the visual field which gave 'on' or 'off' (excitatory or inhibitory) responses to illumination were marked on sheets of paper fixed to the screen. These provided permanent records of the size and shape of the receptive fields and of their position with respect to the fovea and the optic disk.

Single fibres were recorded from the optic nerve with tungsten micro-electrodes (Hubel, 1957). Cathode-follower input and a condenser-coupled pre-amplifier were used in a conventional recording system. In preliminary experiments, not included in this series, the nerve was approached under direct vision from below by a transpharyngeal route and from above by removing one frontal lobe. Both procedures proved tedious, and neither gave good stability. The method finally adopted was a modification of a technique used for single-unit recording within the brain of the unrestrained animal (Hubel, 1960). The nerve was approached from above through the intact brain. A closed system was used to lessen vascular and respiratory pulsations. A hydraulic micro-electrode positioner was oriented by Horsley–Clarke stereotaxic methods. The co-ordinates of the optic nerve were determined from the position of the bony optic foramen, using the average from several spider monkey skulls. During the actual experiment a small hole was made in the skull and an 18-gauge steel tube attached to the positioner was lowered through the brain until its tip was several millimetres above the optic nerve. The space between the tube and the skull was sealed with dental-impression cement. The electrode, held within this outer tube by an insulated 26-gauge hollow needle, was then hydraulically advanced until it entered the optic nerve.

RESULTS

One hundred and twelve optic nerve fibres were studied. In the light-adapted state all fibres showed maintained activity; that is, they discharged impulses in the absence of any stimulus besides the steady uniform background light. No systematic observations were made in the dark-adapted state. Firing patterns resembled, at least superficially, those described for the cat's ganglion cell by Kuffler, FitzHugh & Barlow (1957).

If a small spot of light was projected on the screen one could always find a restricted area over which firing of a fibre could be influenced. This was termed the receptive field of the fibre. Receptive fields had the same general characteristics as those of the cat, described by Kuffler (1953). As in the cat, two main types could be distinguished, both concentrically arranged, one with an 'on' centre and an 'off' periphery, the other with an 'off' centre and an 'on' periphery. Records from an

'off' centre unit are shown in Fig. 1, and illustrate suppression of firing with an 'off' discharge in response to a centred spot, and an 'on' discharge in response to an annulus. Responses from the periphery of receptive fields were often difficult or impossible to elicit in the monkey when stimulus and background intensities were of the same order as those used in work on the cat's retina. However, if both the stimulus and the background luminances were increased by about 2 log units, peripheral responses could usually be obtained. The influence of peripheral parts of receptive

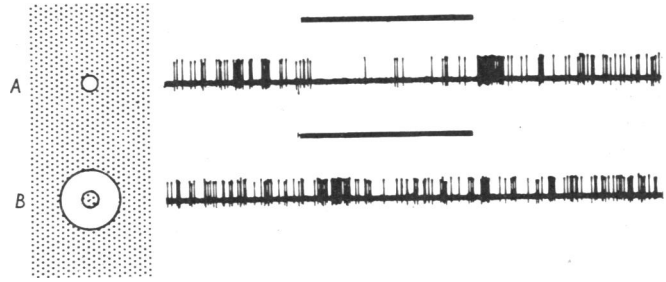

Fig. 1. Responses of an 'off' centre unit to restricted light stimulation. In each example the upper line indicates when the stimulus light is on. *A*, ½° spot of light shone in the centre of the receptive field; *B*, annulus 5° in outside diameter, 2° inside diameter, with its centre over that of the receptive field. Receptive field located on the retina 28° above and 12° nasal to the fovea. Duration of stimuli, 1·5 sec.

fields could be demonstrated even with weaker stimuli, since it was always possible to decrease a centre response by simultaneous stimulation of regions outside the field centre. In Fig. 2 spots of successively larger size were used to stimulate an 'on' centre fibre. The smallest spot did not fill the centre (Fig. 2*A*), and it gave a response considerably weaker than that evoked by a second spot (*B*) which just filled the centre. A still larger spot invaded the periphery (*C*), and the response was now less marked than with the second.

The receptive fields studied were situated in various parts of the retina, ranging between 4° and 56° from the fovea. In any given penetration through the optic nerve from above there was a tendency for receptive fields of the first fibres recorded to be located in the lower quadrants of the visual field. As the electrode was lowered the receptive fields tended to be located higher and higher in the visual field. Otherwise, however, there was little order in the position of fields, and fields of successively recorded fibres were often separated by a considerable distance, in an unpredictable fashion. This is illustrated in Fig. 3 for a particular penetration in which 20 fibres were mapped. From this and other penetrations one had the impression that there was no very detailed topographical

representation in this part of the optic nerve, but only a coarse segregation of fibres from the different quadrants.

The size of receptive field centres ranged from 4 min to 2° of arc. The centres were mapped out by using spots of light which for each field were chosen so as to be small relative to the size of the centre. Relatively high background illumination (1·0 $\log_{10}$ cd/m^2 or more) was used to minimize effects of scattered light. No attempt was made to determine accurately the total extent of each receptive field, but there was little doubt that for

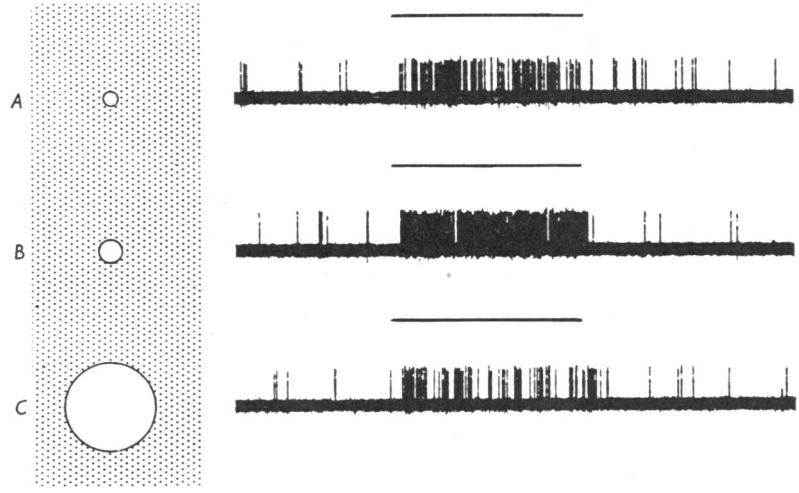

Fig. 2. 'On' centre unit with receptive field 11° above, 4° nasal to fovea. Responses to centred spots $\frac{1}{8}$°, $\frac{1}{2}$° and 4° in diameter. Duration of stimuli, 1·5 sec.

most fields the total diameter was many times that of the centre. There was a clear tendency for receptive field centres near the fovea to be smaller than those in the periphery, although there was considerable variation in centre size at any given distance from the fovea. In Fig. 4 the diameters of 65 field centres are plotted against distance from the fovea. Both 'on' and 'off' centre units were well represented in the series. The number of units is too small to justify any conclusions about the preponderance of one type of field over the other. In particular, the apparent predominance of 'on' centre units over 'off' centre in the region near the fovea is of interest, but again, conclusions can hardly be drawn from such a small sample.

In the present work there was no attempt to make a thorough study of responses to coloured stimuli. However, some preliminary results showed that there are ganglion cells which respond in specific ways to colour. An example is given in Fig. 5. In this unit a 2° spot of white light gave a weak response consisting of suppression of firing followed by a feeble 'off'

discharge (Fig. 5*A*). A decrease in intensity of the white light produced even weaker 'off' responses. With the light source intensity set as in Fig. 5*A*, a blue interference filter was placed in front of the projector. Each time the blue spot of light was shone on the screen it produced a strong 'on' response (Fig. 5*B*). If a red filter was substituted for the blue the firing was strongly suppressed during the stimulus and this was

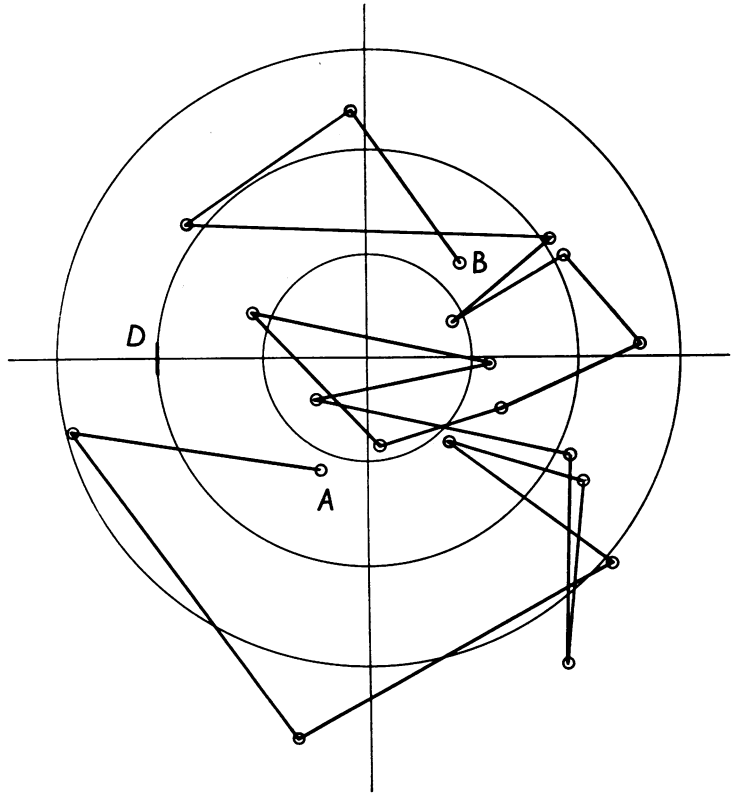

Fig. 3. Location on the visual field of receptive fields of 20 optic nerve fibres recorded in sequence as the electrode was advanced vertically from above through the left optic nerve. The vertical and horizontal lines represent the vertical and horizontal meridia; these cross at the fovea. The optic disk *D* is situated in the temporal field 20° from the fovea. The first unit, *A*, had its receptive field in the lower temporal quadrant of the visual field; the last, *B*, in the upper nasal quadrant.

followed by an 'off' discharge (Fig. 5*C*). It is clear that either filter greatly reduced the radiant flux of the light beam, yet the effects of the stimulus were much enhanced. Moreover, the responses to stimulation with the two different colours were of opposite type. This was true regardless of stimulus intensity or spot size. Two other units studied with monochromatic light gave 'on' responses to wave-lengths shorter than

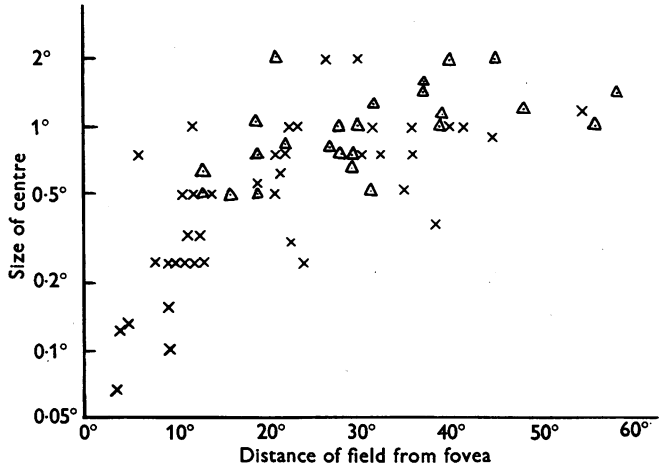

Fig. 4. Diameters of receptive field centres in degrees (logarithmic scale), plotted against distance in degrees of each field from the fovea. ×, 'on' centre units; △, 'off' centre units.

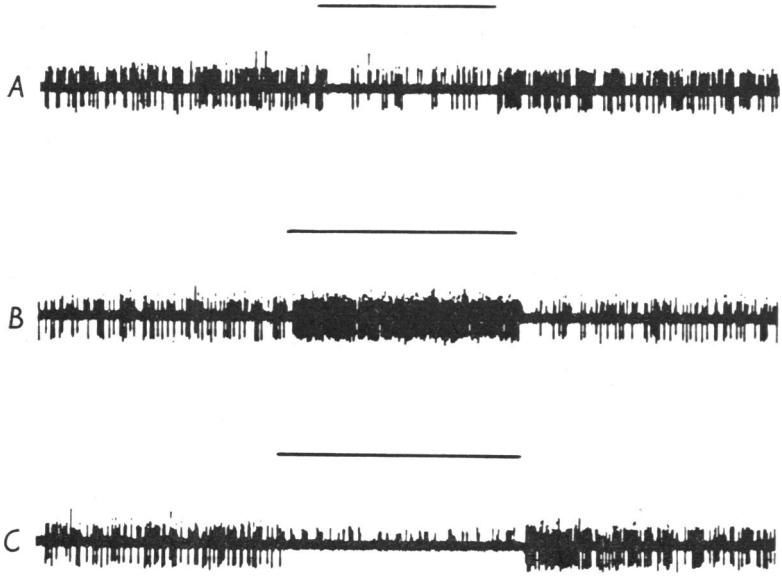

Fig. 5. Response of optic nerve fibre to 2° spot of light shone in centre of receptive field. Location of field, 7° below, 29° temporal to fovea. *A*, white light; *B*, same as *A*, but with blue interference filter (peak transmission 480 mμ) inserted between projector and screen; *C*, same as *A*, but with red interference filter (peak transmission 630 mμ) inserted between projector and screen. Duration of first stimulus, 1 sec.

498 mμ and inhibition with 'off' responses for longer wave-lengths. With 498 mμ a very feeble 'off' response was produced.

It is likely that the units with specific colour responses described above form a small minority of the population of optic nerve fibres, since a number of additional units studied with monochromatic stimuli gave centre responses of constant type, either 'on' or 'off', for all wave-lengths. In these white light gave brisk responses. In this type of ganglion cell, however, there were indications of some variability in the position of spectral sensitivity peaks from one unit to the next, suggesting that they too, conveyed information on colour.

DISCUSSION

From the results presented in this paper it is clear that in the monkey, as in the cat, the receptive fields of retinal ganglion cells are of two main types, one with an 'off' centre and an 'on' periphery, the other with an 'on' centre and an 'off' periphery. The antagonism between centre and periphery of a receptive field is generally not so complete that diffuse light is ineffective.

Fields in the vicinity of the monkey fovea tend to have smaller centres than those in the periphery (Fig. 4). A similar finding has been reported for the cat (Wiesel, 1960). Differences between central and peripheral visual acuity in man may well be related to variations in receptive-field centre size similar to those found in the monkey and cat. In the present study the smallest centre was found for a receptive field 4° from the fovea; this had a diameter of less than 4 minutes of arc. No recordings were made from fibres with receptive fields in the fovea, but it is likely that even smaller field centres are present in this region, since there is less convergence in the pathway from receptors to ganglion cells in the foveal region than in other parts of the retina (Polyak, 1957). Our failure to find foveal fields is probably related to the small diameter of the macular fibres. Moreover, the macular bundle occupies a small part of the optic nerve, and could easily be missed in random penetrations.

The cat has a highly reflectile tapetum behind the retina; in contrast, the retina of the spider monkey is deeply pigmented. With identical stimulus conditions it was generally more difficult to produce a response from the receptive-field periphery in the spider monkey than in the cat. However, it was found that by increasing the stimulus and background luminance by two logarithmic units peripheral responses could consistently be obtained. It is probable that the tapetum of the cat increases the effectiveness of the background illumination, and this may be necessary for the production of a good response from the periphery of the receptive field. It is known, for example, that the influence of the periphery on the

centre response becomes more pronounced with increasing background illumination (Barlow *et al.* 1957).

Several authors have described responses of opposite type to stimulation with light of different colours. Svaetichin (1956) demonstrated membrane hyperpolarization with short wave-lengths and depolarization with long wave-lengths in recordings from cells in the inner nuclear layer of the fish retina (MacNichol & Svaetichin, 1958). Similar results have been reported by other workers (Motokawa, Oikawa & Tasaki, 1957; Tomita, Tosaka, Watanabe & Sato, 1958). In the lateral geniculate body of the rhesus monkey de Valois, Smith, Kitai & Karoly (1958) described units responding with an 'on' discharge to blue light and an 'off' discharge to red light. Wagner, MacNichol & Wolbarsht (1960), recording spike discharges from ganglion cells in the goldfish retina, have since found similar discharge patterns to coloured stimuli.

In the present study of the spider monkey's extra-foveal retina three ganglion cells showed colour responses analogous to those described above. The presence of maintained discharges made it possible to demonstrate inhibitory effects during long wave-length stimuli, in addition to the excitatory responses to short wave-lengths. White light was less effective than monochromatic light, provided the wave-length was either longer or shorter than about 500 mμ. The decreased responsiveness to white light which has been noted also by de Valois (1960) is presumably due to the antagonistic effects of monochromatic light of short and long wave-lengths. This is strikingly similar to the way in which form specificity is obtained in the visual system; shining a restricted light on appropriate parts of a receptive field produces excitatory or inhibitory responses, and the effects tend to cancel when opposing regions are stimulated simultaneously, for instance with diffuse light. In both cases an unspecific stimulus produces less effect on the firing of a single cell than one restricted in form or wave-length, even though it contains more energy.

SUMMARY

1. Receptive fields of retinal ganglion cells were studied in the light-adapted spider monkey. All fields mapped with white light had a concentric arrangement similar to that of cat retinal ganglion cells, with a sharply demarcated 'on' centre surrounded by an antagonistic 'off' periphery, or the reverse.

2. The smallest receptive field centres were found near the fovea, and the size of centres tended to increase with increasing distance from the fovea. The smallest centre had a diameter of 4 minutes of arc (corresponding to about 20μ on the retina) and was located 4° from the fovea; the largest centre had a diameter of 2°.

3. Three ganglion cells out of about 100 responded in a specific way to coloured stimuli. In these cells light of short wave-length produced an 'on' response and light of long wave-length evoked inhibition followed by an 'off' response. Transition between the two types of response occurred at about 500 mμ; light of this wave-length evoked only feeble 'off' responses. Very weak responses were obtained to white light, presumably owing to the antagonism between light of short and long wave-lengths.

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